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Observations on the Behavior and Shell Types of *Cypraea moneta* (Mollusca, Gastropoda) at Enewetak, Marshall Islands[1]

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ABSTRACT: Aspects of the ecology and behavior of knobby and smooth *Cypraea moneta* at Enewetak Atoll, Marshall Islands, are presented. The habitats of *C. moneta* are described. A series of experiments based on aggregation, feeding, and male–female pairing indicated similarities and differences between the smooth and knobby forms. Smooth morphs follow mucous trails only of other smooth-shelled forms of *C. moneta*, whereas knobby morphs follow the mucous trails of both knobby and smooth forms. The most preferred alga of the smooth morphs is *Jania capillacea*, the most abundant species in intertidal areas; and that of the knobby morphs is *Schizothrix calcicola*, a common subtidal species. Male–female pairs constituted 80 percent of the intertidal samples and 81 percent of the subtidal ones. In addition, smooth and knobby morph distributions were investigated in the Line Islands and elsewhere in Micronesia as well as at Enewetak. In all cases the smooth morph was found in the intertidal zone and the knobby morph in the subtidal.

THE MONEY COWRY, *Cypraea moneta* Linnaeus, 1758, is an abundant and easily recognized gastropod throughout the Indo-West-Pacific. A number of names distinguishing subspecies and races have been introduced for the money cowry (see Schilder 1936), and it is generally recognized as a highly variable species.

DISTRIBUTION

Enewetak Atoll consists of an oval chain of 42 islands surrounding a lagoon 40 km long by 32 km wide. Twenty-five of the 42 islands and 28 interisland reefs were sampled for money cowries (Figure 1). Initial observations of the cowries indicated that the animals were not evenly distributed throughout the atoll. Enewetak, the southernmost island, supports the largest population of *Cypraea moneta*, and money cowries in general were found more commonly in waters surrounding the windward islands than the leeward islands. Table 1 lists the islands and interisland patch reefs sampled and indicates the presence or absence of the cowry.

HABITATS

Two major study sites were selected on Enewetak Island, the reef flat and the quarry, representing an intertidal and subtidal habitat, respectively. Other study sites were also distinguished as intertidal or subtidal.

The reef flat at Enewetak, 80 to 120 m in width, is composed of limestone, covered with the cyanophytes *Schizothrix calcicola* and *Calothrix crustacea* in the intertidal zone, and has small heads of the coral *Pocillopora* near the algal ridge. Coralline algae are ubiquitous, but chlorophytes, phaeophytes, and rhodophytes are all represented. A wide (10 to 15 m), shallow pool approximately 35 m from shore and parallel to it extends the length of the bench. *Jania capillacea*, an erect coralline alga, covers most of the pool bottom. The reef flat is exposed at low tide each day. Although a wide expanse of reef flat is available to the money cowry, dispersion is aggregated rather than random or uniform. Cowry density is approximately 10 times greater in the reef flat pool than on the reef flat itself, and dispersion on the reef flat is also aggregated. *Cypraea moneta* density was estimated in 12 areas on Enewetak

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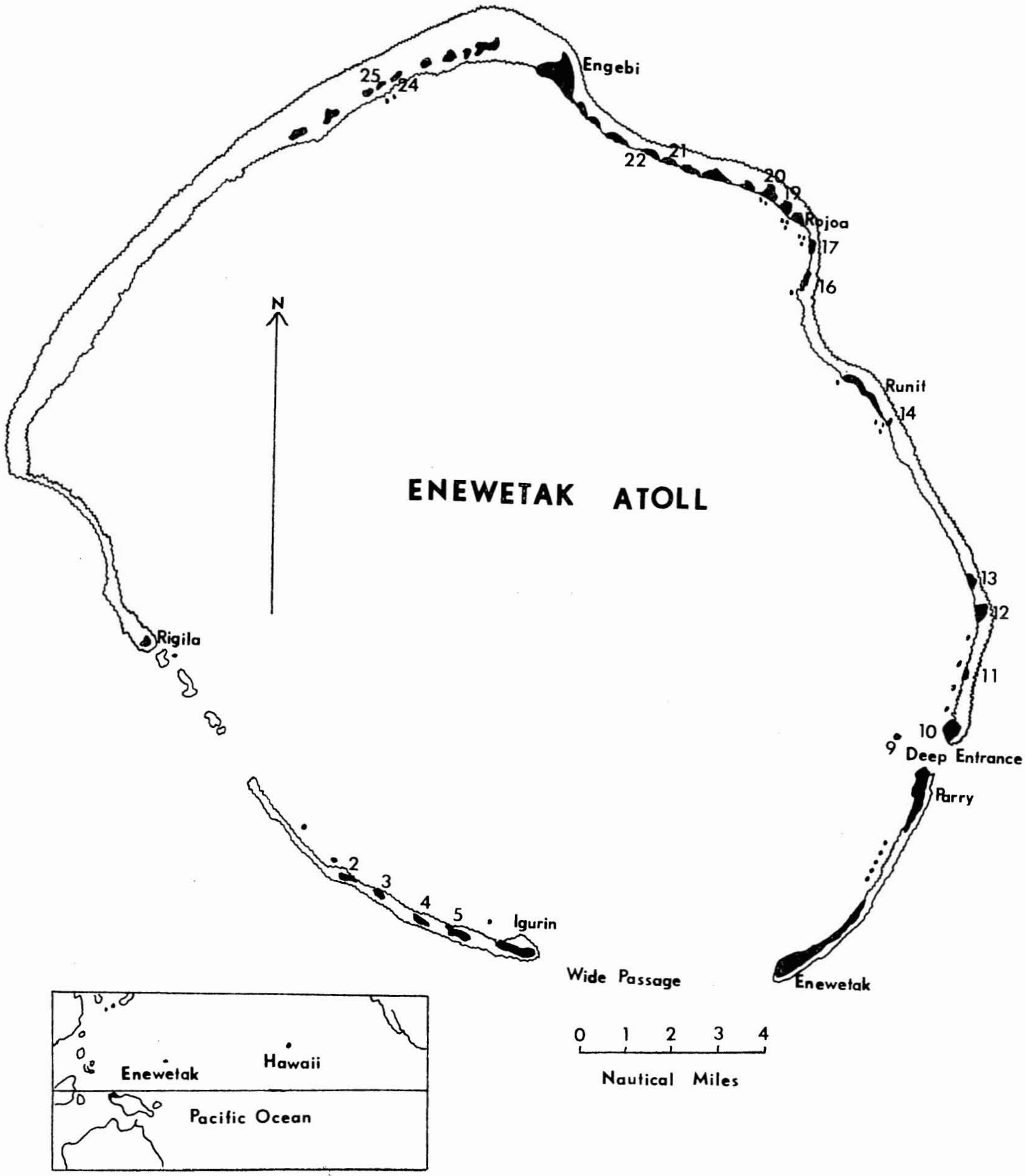

FIGURE 1. Enewetak Atoll. Sites sampled for *Cypraea moneta*. Those sites identified by number only are as follows: 2, Griinien; 3, Libiron; 4, Bogon; 5, Mui; 9, Jieroru; 10, Japtan; 11, Chinimi; 12, Aniyaanii; 13, Chinieero; 14, Zona; 16, Piiraai; 17, Arambiru; 19, Biijiri; 20, Aranit; 21, Rudiyori; 22, Aitsu; 24, Elugelab; 25, Eyybyae. Dots around the inner boundary of the atoll represent patch reefs sampled for *C. moneta*.

Island, i.e., areas 1 to 4 in the reef flat pool, areas 5 to 8 on the reef flat itself, shoreward and adjacent to areas 1 to 4, and areas 9 to 12 in the Enewetak quarry (see Table 2). Specimens of *Cypraea moneta* are rarely, if ever, found singly, but are found most commonly in pairs and occasionally in groups of three or four. Grouped cowries were designated as those not more than 30 centimeters apart.

The Enewetak quarry is a mined portion of

TABLE 1

COLLECTION AREAS FOR *Cypraea moneta*

ISLANDS (REEF FLATS AND SHORES)	*C. moneta* PRESENT (+) OR ABSENT (−)	INTERISLAND PATCH REEFS	NUMBER OF PATCH REEFS *C. moneta* PRESENT (+) OR ABSENT (−) (+)	(−)
Rigila	−	Enewetak-Parry	5	0
Griinien	−	Rojoa-Arambiru	3	0
Libiron	−	Japtan-Chinimi	2	0
Bogon	−	Elugelab-Eyybyae	1	1
Mui	−	Chinimi-Aniyaanii	0	2
Igurin	+	Piiraai-Runit	0	2
Enewetak	+	Aranit-Biijiri	0	2
Parry	+	Runit-Zona	0	2
Jieroru	−	Rigili-Griinien	0	3
Japtan	−			
Chinimi	−			
Aniyaanii	−			
Chinieero	−			
Zona	−			
Runit	−			
Piiraai	−			
Arambiru	−			
Rojoa	−			
Biijiri	−			
Aranit	−			
Rudiyori	−			
Aitsu	−			
Engebi	+			
Elugelab	−			
Eyybyae	−			

the windward reef flat (Figure 2), approximately 45 m wide by 90 m long (Bakus 1967), and varying in depth from 1 to 4 m. Depth in the quarry is reduced by 1 m at low tide. The bottom topography is varied, with small, silt-covered rocks and boulders festooned with various algae (coralline and noncoralline, of which *Schizothrix calcicola* is one of the more common forms) forming major components of the substrate. Large (60 to 245 m²) sandy areas are present, as are areas of dense *Acropora* growth. The cowries are found beneath the loose, rocky substrate in the quarry.

Money cowries were found in two quarries on Engebi Island—in the large quarry on the southern tip of Parry Island, on the windward shore of Igurin Island, and on the windward reef flat of Engebi Island. Twelve of the 28 interisland patch reefs sampled also yielded money cowries (Table 1).

SHELL MORPHS

Two shell morphs, distinguished by the presence or absence of knobs, occur at Enewetak: one type with four knobs, two posterior and two posterior-lateral, and the other type smooth and without knobs (Figures 3–6).

These shell forms are further distinguished by the presence or absence of yellow pigment on their ventral surface. Thus, two varieties in each morphological type are apparent: yellow and white varieties of the smooth and knobby shells. The mean length of all cowries measured at Enewetak Atoll is 1.73 cm and the mean width is 1.38 cm ($N = 324$). No significant difference in length or width was found between the knobbed and smooth forms, but, in both cases, the white varieties are the smaller of the two, as follows. Knobby morph—yellow length greater than white length, P less than 0.0005, $N = 319$; yellow width greater than

TABLE 2

DENSITIES OF *Cypraea moneta* AT ENEWETAK ATOLL

AREA	RANGE	MEAN	SAMPLE SIZE	STANDARD ERROR
Reef Flat Pool				
1	5.56–6.68	6.23	623	0.25
2	2.04–3.64	2.78	278	0.40
3	5.19–5.52	5.27	527	0.11
4	2.23–3.40	2.92	292	0.22
1–4	2.04–6.68	4.30	1720	1.49
Adjacent Shoreward Reef Flat				
5	0.60–0.68	0.63	63	0.02
6	0.20–0.44	0.31	31	0.05
7	0.44–0.56	0.49	49	0.03
8	0.24–0.40	0.33	33	0.03
5–8	0.20–0.65	0.44	176	0.08
Quarry				
9	1.16–1.36	1.25	125	0.04
10	0.24–0.60	0.45	45	0.08
11	1.40–1.60	1.51	151	0.04
12	1.52–1.72	1.62	162	0.11
9–12	0.24–1.72	1.20	483	0.26

NOTE: Densities are expressed in animals per square meter. Densities were obtained at the above areas once each day for 4 consecutive days in a 25-m quadrant.

white width, P less than 0.0005, $N = 294$. Smooth morph—yellow length greater than white length, P less than 0.005, $N = 403$; yellow width greater than white width, P less than 0.0005, $N = 402$).

At no time during the study were the knobby and smooth-shell types found mixed in any of the habitats investigated. The knobby shells occur subtidally (i.e., in the quarries and on the patch reefs) and the smooth shells are found in the intertidal zones where they are subject to alternate exposure and submersion by the tides.

EXPERIMENTAL PROCEDURES AND RESULTS

In an attempt to discern an explanation for the distribution of the money cowries at Enewetak and to delineate further the differences between the knobby and smooth forms, I initiated a series of experiments based on aggregation, feeding, and male–female pairing.

Aggregation

Initial feeding experiments indicated that *Cypraea moneta* follows the mucous trails of other money cowries. To determine if the mucus gives off a scent which is carried in the water and to which the animals respond, I prepared olfactometers (Figures 7, 8) with cowry mucus in one chamber only. Three to four money cowries were allowed to move in the designated chamber to lay down the mucus necessary for the experiment. Laminar flow was initiated so that the animals could follow an odor if it were present. A trial consisted of placing one animal in the olfactometer at the starting point and allowing 15 minutes for each response.

Of the 100 cowries tested, 54 animals moved into the chamber containing the mucus and 46 animals moved into the chamber without the mucus. A chi-square test of $P = 0.45$ indicates no significant difference from the null hypothesis that the cowries cannot sense the presence of mucus by olfaction and suggests that another method, such as contact chemoreception, is necessary for mucous trail detection.

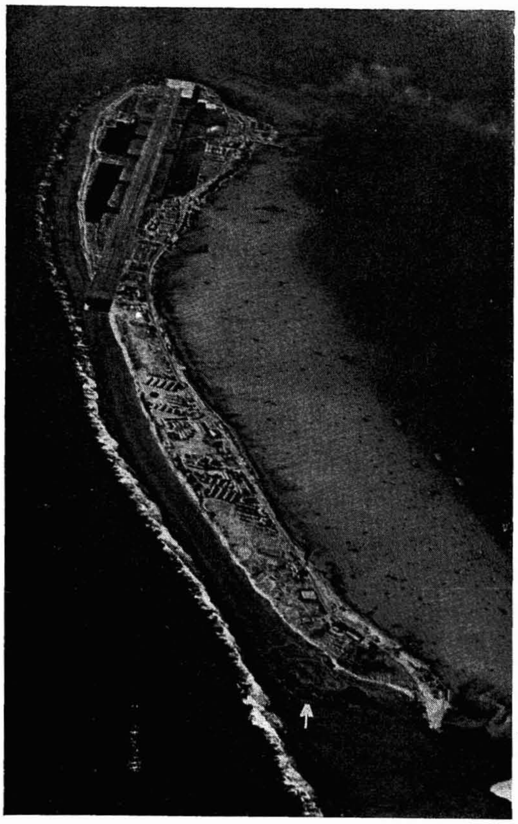

FIGURE 2. Aerial photograph of Enewetak Island and reef flat. Arrow points to Enewetak quarry.

A controlled experiment conducted without mucus in the olfactometer indicated that the animals were not likely to move more readily into one chamber than into the other. Twenty-eight of 50 cowries moved into the right chamber of the olfactometer, whereas 22 moved into the left chamber.

I elaborated the mucous trail experiments to determine if there was any difference in the responses of the money cowry to the mucous trails of the different morphs within the species. The cowries were placed one at a time in olfactometers containing only running seawater and were given 15 minutes to move about in the container. Their paths were mapped on data sheets. New animals were then inserted without the olfactometers being washed and their movements were recorded. I used a maximum of six animals in one olfactometer; then I scrubbed it with a sponge to remove the mucus before starting again.

Fifty-seven of the animals tested were of the smooth morph, and, of these, eight did not move. Of the remaining 49 animals, 17 initially crossed the mucous trail of a knobby morph but did not follow it. However, all 32 of the smooth-shelled animals that contacted the mucous trails of other smooth-shelled cowries followed the trail to its end. Knobby morphs, on the other hand, responded positively to the mucous trails produced by both smooth and knobby morphs. Of the 12 knobby individuals tested, six came into contact initially with the mucous trail of a smooth morph, and four of these followed the trails to their ends. Four of the remaining six cowries encountered mucous trails of other knobby individuals and followed them, whereas the other two did not encounter any trails.

In a similar experiment, 16 knobby snails were allowed to move only across the width of the olfactometers, with one cowry per instrument. One smooth-shelled snail was placed downstream in each of the 16 olfactometers and allowed to move up the channel. Sixteen smooth-shelled cowries were also allowed to move across the width of the sixteen olfactometers and the reactions of the knobby forms were recorded. The results of these tests confirm the findings of the previous experiments: none of the 16 smooth morphs responded to the mucous trails of the knobby morphs, whereas six of the 16 knobby forms turned at the mucous trails of the smooth forms.

The mucous trail experiments suggest not only that chemoreception is a factor in the orientation of these animals, but that there is a chemical difference, perhaps genetically determined, in the mucus of the two different morphs of *Cypraea moneta*.

Feeding

Twenty-six species of algae were found in the quarry and on the reef flat of Enewetak Island, but only six species were common to both areas (Table 3). In the pool on the reef flat the highest density of *C. moneta* was found on the coralline rhodophyte *Jania capillacea*. The distribution of *Jania* on the reef flat itself is

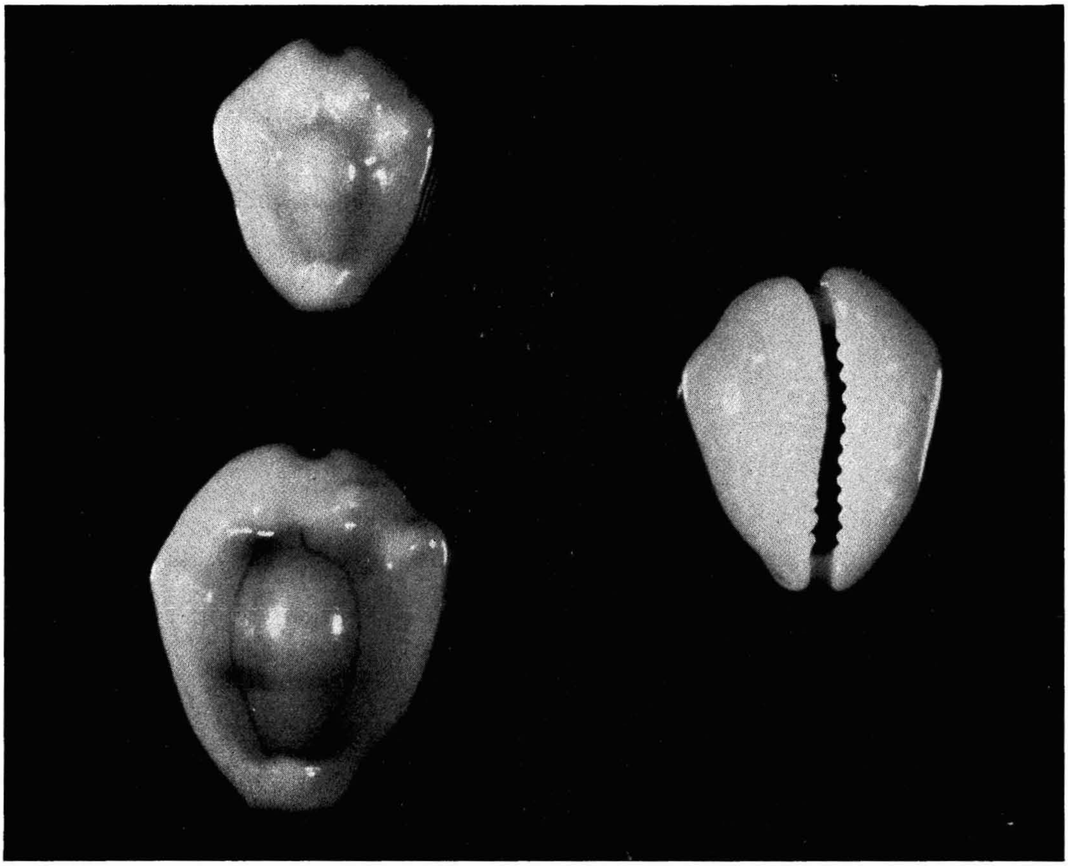

FIGURE 3. The yellow knobby phenotype of *Cypraea moneta* (2.4 × life size).

patchy, and cowries found in this area are usually on this red alga. Do these cowries show a feeding preference for *Jania*? Can they sense the presence of this alga and, if so, does this lead to the *C. moneta* aggregations found on the reef flat?

A preliminary experiment was conducted to determine whether the cowries could chemically sense the presence of algae. I tested the cowries in an olfactometer, using water pumped directly from the lagoon, and offered several species of algae in only one chamber of the apparatus. The algae were switched to the opposite side of the olfactometer at the beginning of each trial and each olfactometer was checked with food coloring to ensure laminar flow.

Of the 100 cowries tested, 97 responded positively by moving up the olfactometer to algae present in a single chamber. These data suggest that the money cowry responds to food by olfaction. Further experiments were set up to determine the preferences exhibited by the different shell types. Feeding preference experiments were conducted by placing two species of algae in an olfactometer, one species in each chamber. The knobby and smooth-shelled types were tested with those species of algae found in the environment from which they had been removed. A trial consisted of placing one animal in an olfactometer and giving it 30 minutes to respond. Each was tested only once and its choice recorded. Nonresponding animals (those not moving), 89 out of the 1464 tested, were not tested further. Twenty-five trials were run to determine the preference of a morph for the two species of algae. Laminar flow was ensured and the olfactometer washed after each trial to remove mucous trails.

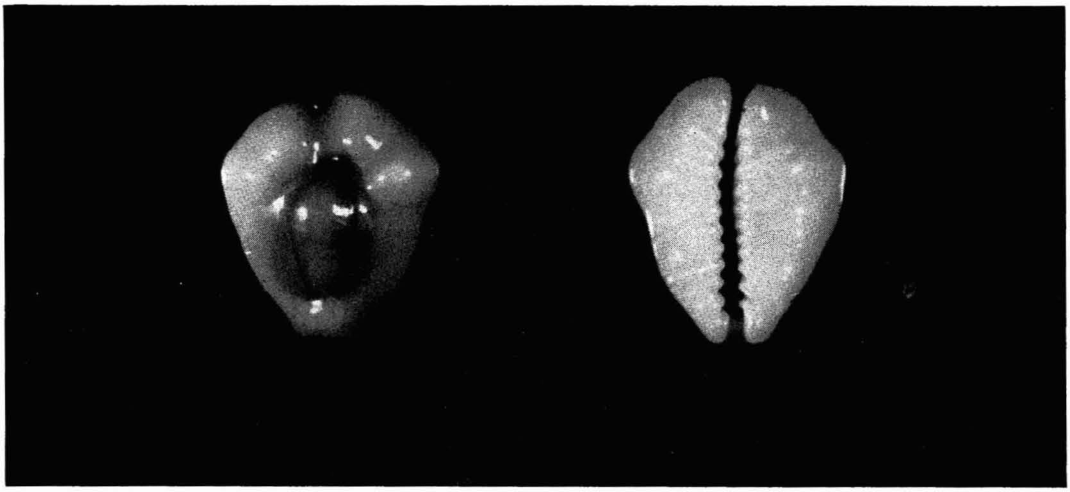

FIGURE 4. The white knobby phenotype of *Cypraea moneta* (2.2 × life size).

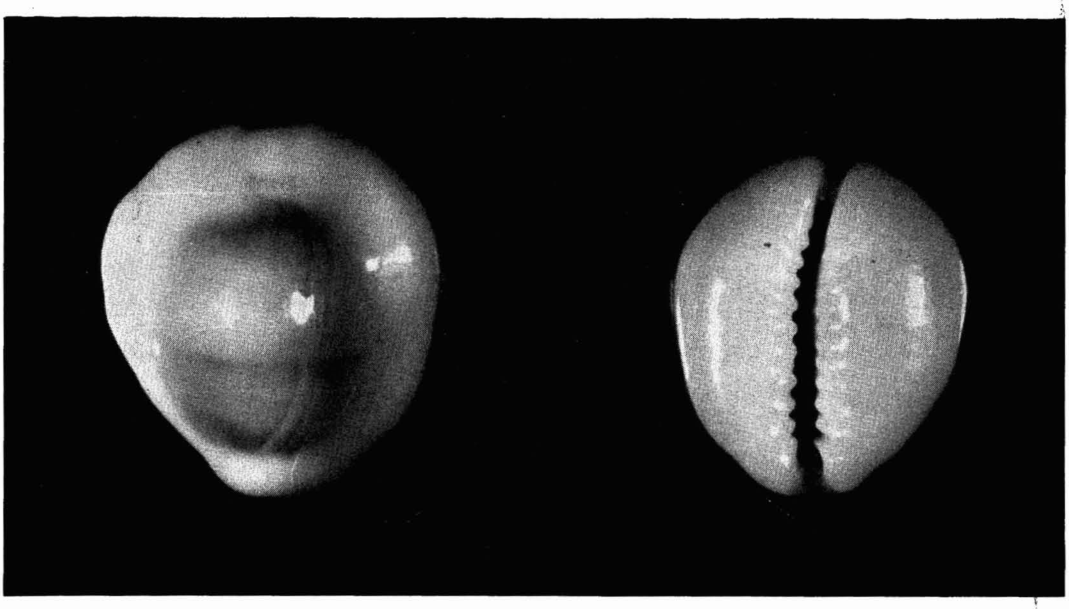

FIGURE 5. The yellow smooth phenotype of *Cypraea moneta*.

The most preferred species of the smooth morphs was *Jania capillacea*, the most abundant alga on the reef flat; that of the knobby morphs was *Schizothrix calcicola*, a common form in the quarry. The five algal species most commonly chosen by the smooth morph of *Cypraea moneta* are listed in order: (1) *Jania capillacea*, $P = 0.036$; (2) *Schizothrix calcicola*, P less than 0.005; (3) *Cladophoropsis* sp., $P = 0.008$; (4) *Dictyosphaeria versluysii*, P less than 0.005; (5) *Microdictyon okamurai*. The knobby morphs chose, in order: (1) *Schizothrix calcicola*, $P = 0.07$; (2) *Polysiphonia* sp., P less than 0.005; (3) *Lyngbya* sp., $P = 0.07$; (4) *Cladophoropsis* sp., $P = 0.018$; (5) *Dictyosphaeria versluysii*. The above P values are the statistical probabilities of number two being chosen over number one, number three being chosen over

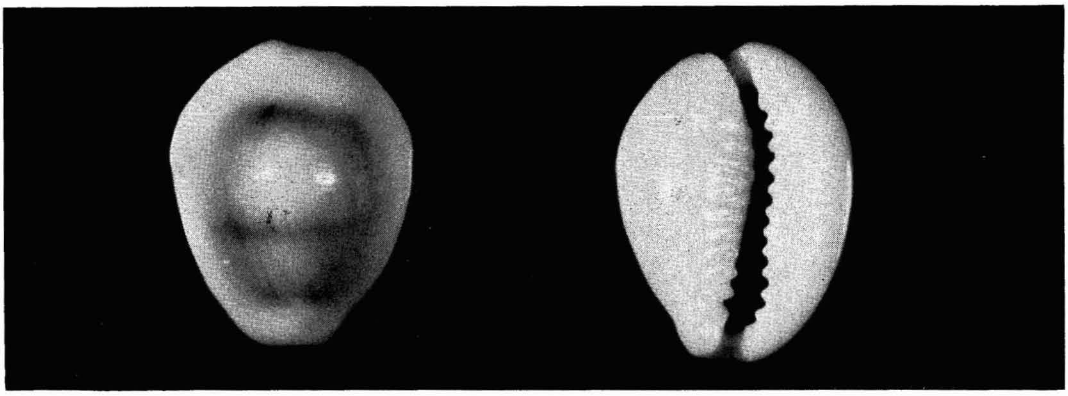

FIGURE 6. The white smooth phenotype of *Cypraea moneta* (2.3 × life size).

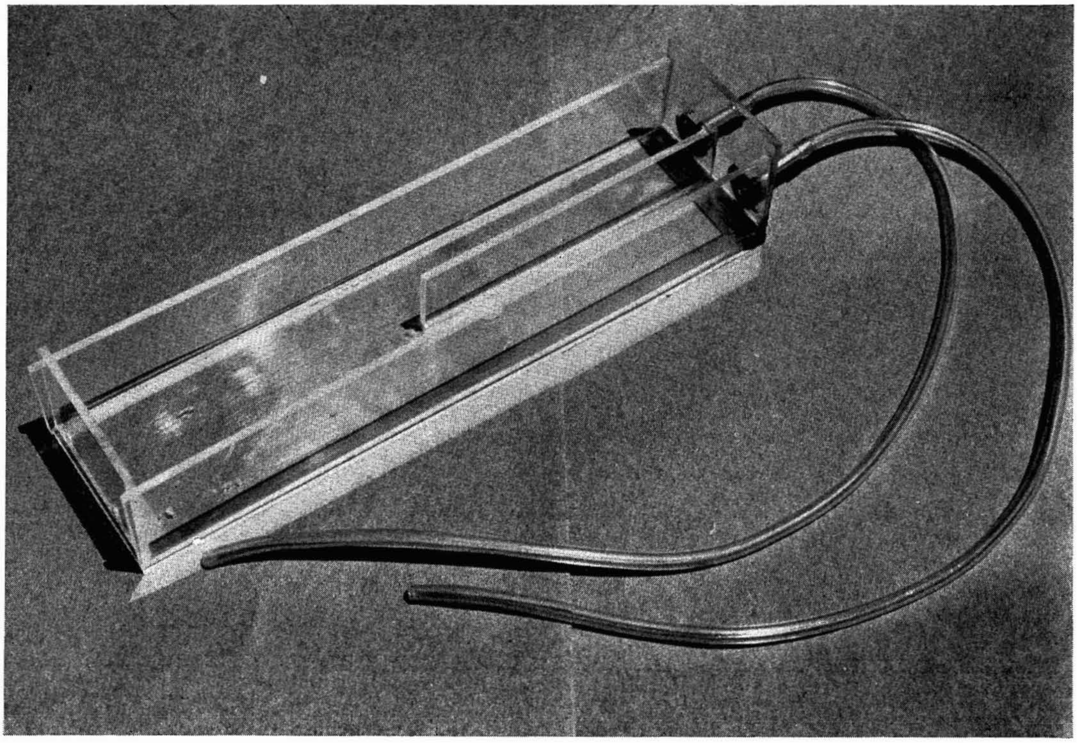

FIGURE 7. The type of olfactometer used in the feeding preference and mucous trail experiments.

number two, etc., and were calculated with a chi-square analysis adjusted for small sample sizes (Snedecor and Cochran 1969: 125–128). The null hypothesis is that, if there is no preference, the number of choices should be equal for both species of algae tested.

Male–Female Pairing

Because the cowries appeared to occur most commonly in pairs, I made a series of tests to see if the pairs comprised a male and a female. Sexual dimorphism is not apparent in the shells, and sex had to be determined anatomically.

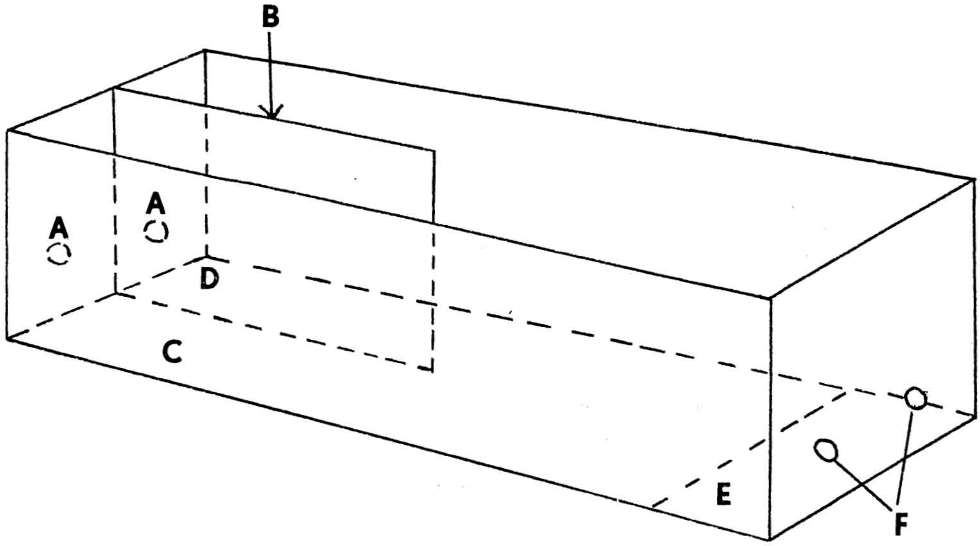

FIGURE 8. Schematic diagram of the olfactometer. *A*, water entrance; *B*, chamber partition; *C*, left chamber; *D*, right chamber; *E*, starting position; *F*, water exit.

Five hundred cowries, 250 each from the quarry and the reef flat, were collected at random and sexed. Males constituted 50 percent of the reef flat sample and 51 percent of the quarry sample. Fifty-five pairs of cowries were then collected from the reef flat and the quarry, respectively, and these cowries were sexed. Eighty percent of the pairs from the reef flat and 81 percent of the pairs from the quarry consisted of male–female pairs. These figures give higher values than would be expected from male–female ratio of the population structure. Chemoreception may aid in the formation of pairing, with the cue possibly being that of the mucous trails of other cowries.

DISCUSSION AND CONCLUSIONS

The occurrence of knobby morphs and smooth morphs is not limited to Enewetak but appears to be widespread throughout Micronesia and also at Fanning Island in the Line Islands. Table 4 lists the districts of Micronesia sampled for money cowries (by myself and/or Dr. E. Alison Kay, University of Hawaii), the number of collections, the number of specimens per collection, the type of habitat, and the cowry morph present. As at Enewetak, knobby and smooth morphs appear to be associated with particular habitats—knobby morphs with subtidal areas and smooth morphs with intertidal areas. Intermediate forms were found at only two collection sites, one at Fanning Island, the other in Palau. The intermediate cowries at Fanning were collected from a sloping area, mainly subtidal, where exposure occurs only a few weeks during the year. At Palau the intermediate cowries were collected from a subtidal slope on Koror, between the islands of Koror and Babelthuap, an area also intermediate between intertidal and subtidal, and one having strong currents moving through the channel with the changing of tides.

The major generalization which can be drawn from this paper is that the distribution of the shell forms of *Cypraea moneta* appears to be associated with the habitats present (intertidal and subtidal). Orr (1959) noted a similar distribution of shell forms in the related *Cypraea annulus* at Zanzibar but did not pursue the question of the terminology which might be applied to the various forms.

The two forms of *C. moneta* are related and raise two interesting questions: (1) how are these cowries related, and (2) what terminology should one use when discussing them?

TABLE 3

ALGAE PRESENT ON THE WINDWARD REEF FLAT AND IN THE QUARRY OF ENEWETAK ISLAND

TAXA	QUARRY	REEF FLAT POOL	REEF FLAT INSHORE OF POOL
Chlorophyta			
Caulerpa sp.	+		
Cladophora sp.	+	+	
Cladophoropsis sp.		+	
Dictyosphaeria versluysii (Weber van Bosse)	+	+	
Halimeda sp.	+		
Microdictyon okamurai (Setchell)		+	
Neomeris sp.	+		
Valonia aegagropila (J. Ag.)		+	
Valonia ventricosa (C. Ag.)		+	
Phaeophyta			
Dictyopterus sp.	+		
Dictyota sp.	+		
Ectocarpus breviarticulatus (J. Ag.)			+
Padina sp.			+
Pocockiella sp.	+		+
Rhodophyta			
Asparagopsis sp.		+	
Centroceras clavulatum (C. Ag.) Montagne		+	+
"Gelids"	+		
Herposiphonia sp.	+		+
Hemitrema sp.	+		
Jania capillacea (Harvey)		+	+
Polysiphonia sp.	+		
Porolithon sp.	+	+	+
Spiridia sp.	+		
Cyanophyta			
Calothrix crustacea (Thur.)			+
Lyngbya sp. (Agardh)	+		
Schizothrix calcicola (Agardh) Gomont	+		+

Although various names have been assigned to the variations in shell form exhibited by *C. moneta* (Schilder 1936) it is clear from this study that the shell forms can be associated largely with the environment.

Terms commonly utilized to distinguish among intraspecific morphological forms are: varieties, subspecies, geographic races, polymorphs, polytypic races, and polyphenotypes. A morphological deviant from the main population may be termed a variety, which is too broad a term to be applied to the money cowries. Differences can be found between any two shells if one scrutinizes them long enough. Every organism which is a subspecies has a formal trinomen; these particular money cowries do not. Other money cowries such as *Monetaria monetoides harrisi* Iredale, 1939, *M. moneta endua* Schilder & Cate, 1943, *M. moneta erua* Schilder & Cate, 1943, and *M. moneta etolu* Schilder & Cate, 1943, have been given a trinomen because they exhibit major differences in shell form and have only a limited distribution in the Pacific region. Geographic races are separated by physical barriers. The habitats of the money cowry may be considered adjacent, continuous, and not at all isolated from each other; therefore, they cannot be considered as geographic races. Polymorphism and polymorphs occur within a species when morphological variation is due to gene differences (Mayr 1963). In the Hawaiian Islands, the marine prosobranch *Littorina picta* exhibits an excellent example of polymorphism, and it has

TABLE 4

HABITAT DISPERSION OF *Cypraea moneta*

AREA	NUMBER OF COLLECTIONS	NUMBER OF INDIVIDUALS
Micronesia		
Majuro, Windward (Is)	1	91
Majuro, leeward (Is)	1	27
Ponape (Sk)	1	62
Palau (Sk)	4	27, 7*, 3, 1
Yap (Sk)	1	10
Fanning Island		
East Island (Is)	1	13
North Pass (Sk)	2	42, 10
Station Reef (Sk)	1	11*
English Harbor (Sk)	8	54, 37, 30, 18, 14, 14, 7, 2
Enewetak Atoll		
Enewetak Quarry (Sk)	10	50 each
Enewetak Reef Flat (Is)	10	50 each
Engebi Quarry (Sk)	1	16
Engebi Reef Flat (Is)	1	62
Interisland Patch Reefs (Sk)	28	7, 7, 6, 5, 5, 5, 5, 4, 2, 1, 1, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0

NOTE: Sk, subtidal samples with knobby shells; Is, intertidal samples with smooth shells.
* Intermediate shell forms.

been demonstrated that ecological forces determine the distribution of its different morphs (see Struhsaker 1968). Different forms of this mollusk are selected for, or against, depending on their shell sculpture. In this case, during a time period, all morphs or more than one morph are found mixed within the habitat. Because the two morphs of *Cypraea moneta* are never found together, the term polymorphism is not applied to the money cowry. The term polytypic race (Mayr 1963) is utilized for specially adapted populations within a species in any ecologically marginal area, whether this occurs in the center of the species range or at its periphery; polytypic races are characterized by actual or potential genetic continuity of allopatric populations (Mayr 1963). Areas in which *C. moneta* are found are by no means marginal. I believe, however, that *C. moneta* populations are genetically continuous or have the potential to be genetically continuous and are, by definition, allopatric populations. Polytypic races nearly defines the situation as it is, but I feel that polyphenism better describes the way in which the money cowry is dispersed in relation to its surroundings. Polyphenism is the occurrence of several phenotypes in a population, the differences between them not being the result of genetic differences. I do not believe that the morphs of *Cypraea moneta* are genetically different, but that environmental forces are responsible for the activation or inhibition of certain genes. In the case of the money cowry, I suggest that knob formation is inhibited by forces in the intertidal area, perhaps current strength altering the mantle position on the shells of the animals. Thus, my data lead me to believe that the most useful way to discuss the different morphs of *C. moneta* is to refer to them as polyphenotypes.

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LITERATURE CITED

BAKUS, G. J. 1967. The feeding habits of fish and primary production at Eniwetok, Marshall Islands. Micronesica (J. Univ. Guam) 3: 135–149.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Belknap Press, Cambridge, Massachusetts. xiv+797 pp.

ORR, V. 1959. A bionomic shell study of *Monetaria annulus* (Gastropoda: Cypraeidae) from Zanzibar. Not. Nat. Acad. Nat. Sci. Philadelphia 313. 15 pp.

SCHILDER, F. A. 1936. Revision of the genus *Monetaria* (Cypraeidae). Proc. Zool. Soc. London 106 (2): 1113–1135.

SNEDECOR, G. W., and W. G. COCHRAN. 1969. Statistical methods. Iowa State University Press, Ames. xiv+593 pp.

STRUHSAKER, J. W. 1968. Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia: Mesogastropoda). Evolution 22 (3): 459–480.